



## Do Equids Live longer than Grazing Bovids?

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# 1    **Do equids live longer than grazing bovids?**

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14 **ABSTRACT**

15 A large part of the diversity of longevity and actuarial senescence (i.e. the progressive decline  
16 of survival probabilities with age) across vertebrates can be related to body size, phylogeny  
17 and the species' position on the slow-fast continuum of life histories. However, differences in  
18 mortality patterns between ecologically similar species, such as bovids and equids, remain  
19 poorly understood. Equids are commonly understood to outlive bovid species relative to their  
20 body mass, despite very similar feeding niches. Comparing survival patterns of 13 bovid and  
21 10 equid sub-species, our findings confirm that equids outlive bovid species, with a higher  
22 adult survival rate and a delayed onset of senescence for equids, but no difference of rate of  
23 actuarial senescence. These differences are associated with a slower generation time and  
24 longer inter-birth interval, due to a longer gestation period, for equids compared to bovids.  
25 Finally, our results suggest that all biological times (i.e. all life history traits expressed in time  
26 units) have evolved synchronously in bovids, whereas in equids gestation time and inter-birth  
27 interval either were never in synchrony with, or have slowed down relative to other biological  
28 times. Our findings suggest the existence of different selection pressures, or different  
29 constraints, on specific time-related traits between these two mammalian orders.

30 **Keywords:** actuarial senescence; biological times; demography; pace of life; slow-fast con-  
31 tinuum

32 **Running head:** Equids vs bovids' actuarial senescence

33 **Word count:** 5734 words

## 34 INTRODUCTION

35 Actuarial senescence, defined as the progressive decrease of survival with increasing age, is a  
36 ubiquitous process across the tree of life (Nussey et al. 2013; Jones et al. 2014). Striking dif-  
37 ferences in actuarial senescence and lifespan have been found in related species, such as the  
38 naked mole rat (*Heterocephalus glaber*) which lives nine times longer than similar-sized ro-  
39 dents (Buffenstein 2008; Ruby et al. 2018). Such differences across phylogenetically related  
40 species or across species sharing the same lifestyle remain poorly understood and are current-  
41 ly attracting much interest (Gorbunova et al. 2014; Healy et al. 2014). However, little work  
42 has been done, so far, to understand variation in senescence between distantly related species  
43 that have converged into closely similar niches.

44 Here we compare patterns of actuarial senescence (hereafter ‘senescence’) between  
45 taxa from two orders of mammals, equids (Perissodactyl) and grazing bovids (Artiodactyl),  
46 which are large herbivores whose evolution separated 55 million years ago (Janis 1976).  
47 Many of the grazing species, among the equids and bovids, have evolved in parallel in similar  
48 environments since the Miocene (Janis 1976). These two groups of herbivores display evolu-  
49 tionary convergence in key morphological characters, such as elongated limbs and hyp-  
50 sodonty (i.e. the height of the molar teeth), and occupy similar feeding niches despite having  
51 different digestive systems (Janis 1976). Moreover, it is commonly assumed that horses live  
52 longer than cattle. For instance, in the AnAge database (Tacutu et al. 2012), the maximum  
53 lifespan recorded for the seven species of extant equids ranges from 30.1 years for kiang  
54 (*Equus kiang*) to 57 years for domestic horse (*E. caballus*), while for grazing bovids the max-  
55 imum longevity recorded is 36.1 years for the lowland anoa (*Bubalus depressicornis*).

56 Among bovids, grazers live longer and senesce later and more slowly than do brows-  
57 ers, both in the wild (Gaillard et al. 2008) and in captive populations (Lemaître et al. 2013;  
58 Tidière et al. 2015). This difference is even more marked in captivity, probably because the

food provided in zoos is more suitable for grazers than for browsers (Müller et al. 2010, 2011; Lemaître et al. 2013; Tidière et al. 2015). The extant equids are typically grazers (Schulz and Kaiser 2013), while bovids comprise species ranging over a continuum of dietary niches from grazers to browsers (Hofmann 1989; Gordon and Prins 2008); therefore, we only used data from grazers among the bovids to perform a valid comparison of longevity and senescence patterns across these groups. The use of captive populations allows patterns of longevity and senescence of the two orders to be studied independently of environmental variation, which is likely to be a key driver of mortality patterns (Gaillard et al. 1993). In captivity, animals are protected against starvation and predation, and competition for resources is minimal or absent. Using a dataset of 15 species (comprising 23 species or subspecies; 13 bovids and 10 equids) living in captivity, we found strong support for longer longevity in equids than in bovids after taking into account allometric relationships. This difference is associated with higher adult survival and delayed onsets of senescence for equids, but there is no difference between the two orders in the rate of actuarial senescence.

A major axis of variation in longevity and senescence across species is included in the slow-fast continuum of the life histories (Stearns 1983). Indeed, variation in life history traits among species is structured along a continuum of biological times that contrasts species with short longevity, early reproduction, high annual fecundity, and early onset and/or fast rates of senescence (at the continuum's fast end), with species with long longevity, delayed reproduction, low annual fecundity, and late onset and/or slow rates of senescence (at its slow end, e.g. Gaillard et al. 1989; Ricklefs 1998, 2010; Jones et al. 2008; Bronikowski and Vleck 2010). We, therefore, assessed whether observed differences of longevity between bovids and equids simply correspond to a different ranking over the slow-fast continuum as measured by the generation time (Gaillard et al. 2005). Two plausible, but different, demographic scenarios were tested: (1) all biological times or (2) only certain biological times are slower in equids

than in bovids, leading to a difference in the pace of life (as represented by longer generation times in equids). Causes of the differences could be selection pressures for a slower pace of life in equids, or for a faster pace of life in bovids, with potentially different selection pressures and constraints acting on the different components of generation time. Evolutionary processes behind the differences in extant equids and bovids are discussed.

## **METHODS**

### **Datasets**

The life tables of the zoo populations were compiled from the Species360 database, which contains data since 1817 from more than 1,000 member institutions in over 90 countries worldwide. Information on sex, dates of birth and death is available for each individual. Assuming that the total number of individuals living in zoos for a given species corresponds to a worldwide meta-population, we computed population parameters for species living in captivity. We constructed life tables available for females of equid and grazing bovid species for which the exact dates of birth and death are known. We considered all dead and living females but, to avoid any overestimation of the species' longevity due to some individuals never being recorded as dead, we removed individuals still alive in January 2014 with an age more than 125% older than the maximum age at death reported in AnAge, as longevity can be longer in zoos today than 20 years ago due to the improvement of captive conditions (e.g. Wich et al. 2009 for orang-utan, *Pongo* sp.). To ensure that the inclusion of all cohorts did not bias the results, the same analyses were done with cohorts for which all individuals are dead, defined as cohorts for which all females were already dead in January 2014. For some species, wild-type and domestic populations are kept in zoos (e.g. *Bos javanicus*). For these species, only the wild-type taxa were retained in the analyses. We obtained a final dataset of 23 taxa including 13 grazing bovids and 10 equids (Fig. S1).

## Survival and actuarial senescence metrics

For each species, five different, and complementary, metrics were used to assess senescence patterns: maximum age at death, longevity, average adult survival rate, age at the onset of senescence and rate of senescence. The maximum age at death was determined as the maximum age at death observed in the database (Table S1). For the four other metrics, we built the capture history of each female and obtained age-specific survival estimates using the CMR (capture-mark-recapture) software E-SURGE (Choquet et al. 2009) (see appendix S1 for more details). From these age-specific survival estimates, we calculated the proportion of individuals alive at each age ( $l_x$ , with  $l_0=1$ ) and longevity was measured as the age at which 90% of individuals from the initial cohort were dead (age  $x$  at which  $l_x=0.1$ ) (Table S1). This avoids spurious estimates due to different sample sizes or exceptionally long lives of a few individuals (Moorad et al. 2012).

To assess actuarial senescence, we fitted different age-dependent models from birth onwards: constant survival, two age-classes, full age-dependence, and several Gompertz models with different onsets of actuarial senescence (see appendix S1 for more details). To select the best survival model, we used a model selection procedure based on the Akaike Information Criterion (AIC, Burnham and Anderson 2002). For each species, we retained the model with the lowest AIC (Table S2). For 10 of the 13 bovids and 9 of the 10 equids, a Gompertz model provided a better fit than either the constant or the two-age class model, and was more parsimonious than the full age-dependent model (Table S2). The age at which survival begins to decline, corresponding to the age at the onset of senescence (Péron et al. 2010), varied among taxa (Table S1). In addition, from the selected Gompertz model, we measured both adult survival rate as the mean annual survival estimated between 1 year of age and the onset of senescence (Table S1) and rate of senescence as the exponential rate of mortality increase with age (Table S1). On a logit scale, age variation in survival was,

therefore, constrained to be linear from the age at the onset of senescence onwards (Gaillard et al. 2004). For four species (*Connochaetes taurinus albojubatus*, *Kobus kob leche*, *Syncerus caffer* and *Equus quagga boehmi*), the full age-dependent model had a lower AIC than any Gompertz model. For these four taxa, only the maximal age at death and longevity were analyzed.

### **Mean values for the traits of adult females in each taxon**

Mean body mass (BMA, in kg) for adult females was extracted from the literature (Table S3) to correct for allometric constraints. When available, body mass measures from wild populations were preferred.

The pace of life of a given taxon was measured as the generation time using the method described in Gaillard et al. (2005) (see appendix S1 for more details). As life history traits with a currency of time, we considered gestation length (GL, in days), age at first parturition (AFP, in days), and the inter-birth interval (IBI, in days) to test the potential difference of life history strategy between equids and bovids (Table S3). Values for GL, AFP, and IBI were extracted from the literature (Table S3).

### **Analyses**

We first tested the differences in survival and actuarial senescence metrics between bovids and equids, accounting for body mass, because large species live longer and senesce later and more slowly than small species (e.g. Jones et al. 2008; Ricklefs 2010; Lemaître et al. 2014; Tidière et al. 2015). Dependent variables included maximum age at death, longevity, adult survival rate, onset of senescence and rate of senescence. The full models included body mass and order (as factor) as independent variables.

In a second step, we tested whether the differences in survival and actuarial senescence metrics between bovids and equids parallel a difference in life history strategy. For



each trait corresponding to a biological time included in the study (i.e. generation time, gestation length, inter-birth interval and age at first parturition), the full models included body mass and order (as factor) as independent variables.

In a third step, we ran a normed Principal Component Analysis (PCA, package ‘*ade4*’, (Dray and Dufour 2007) for bovids (N=5 taxa) and equids (N=7 taxa) separately, with generation time, longevity, age at first parturition, gestation length and inter-birth interval as biological times. Under scenario 1, all biological times in both equids and bovids should contribute equally to the overall time scale (i.e. equi-correlation sensu Morrison 1967), which corresponds to the slow-fast continuum (Gaillard et al. 2016). In contrast, under scenario 2, equi-correlation should not be observed, meaning that the overall time scale is driven more strongly by some specific biological times and less by others.

Analyses were not corrected for phylogenetic relatedness beyond the inclusion of order as a factor because the number of species was rather small and did not allow estimating reliably the phylogenetic inertia. All traits were log-transformed to improve the normality of the distributions, except order (entered as a factor) and adult survival rate that was logit-transformed. Analyses were performed using the linear model (lm) in R version 2.14.0 (R Development Core Team 2016) and parameter estimates are given  $\pm$  SE and/or 95% confidence intervals.

The datasets generated during and/or analysed during the current study are available in the supplementary data. However, the raw longevity dataset used to compute the survival and senescence metrics are available upon request and with permission of Species360.

## RESULTS

### Differences in survival and actuarial senescence parameters

As expected, all survival metrics (i.e. maximum age at death, longevity and adult survival

rate) increased with adult body mass (Tables 1 and S4, Fig. 1). Moreover, for a given body mass, equids had a maximum age at death 6.9 years (95%CI [3.9; 10.0], Table 1, Fig. 1A) longer and a longevity 5.5 years (95%CI [2.4; 8.6], Table 1, Fig. 1B) longer than bovids. Equids also had a higher adult survival (+ 0.018, 95%CI [0.002; 0.035], Table 1, Fig. 1C) than bovids. Order was the only factor included in the selected model to explain variation observed in the onset of actuarial senescence (Table S4): equids began to senesce 5.89 years (95%CI [2.33; 9.44], Table 1) later than bovids, irrespective of body mass (Fig. S2). Finally, observed variation in the rate of senescence was explained only by the age at the onset of senescence (Table S4), with the rate of senescence increasing when the onset was late (Table 1, Fig. S3). However, the model also including body mass was competitive ( $\Delta$  AIC = -1.31, Table S4) that for a given onset of senescence, the rate of senescence tended to decrease with increasing body mass ( $\beta$  = -0.342 ± 0.196). There was no detectable difference between bovids and equids in the rates of senescence in any of the models.

Using only extinct cohorts in the dataset results were similar to those obtained with all individuals (Tables S5-S7): the order factor was included in the selected models for all survival metrics, which indicates that equids outlived bovids and had higher adult survival. For senescence metrics, the selected models did not include body mass or the order factor. However, for the onset of senescence, the AIC of the model with order as a factor was only 0.51 AIC units lower than the selected model with equids senescing 4.21 ± 1.57 years later than bovids. Finally, the rate of senescence was only influenced by the onset of senescence.

## **Differences in life history traits**

As expected, irrespective of the order, the four biological times were positively correlated to adult body mass (Table 2 and S8, Fig. S4). Bovids had shorter generation times (by 2.31 years, Fig. S4A), shorter gestation lengths (by 89.2 days, Fig. S4B) and shorter inter-birth

intervals (by 157.3 days, Fig. S4C) than equids. On the other hand, no detectable difference of age at first parturition was found between equids and bovids (Fig. S4D, Tables 2 and S8).

## **Evolutionary pathways**

In absence of species-specific selection pressure on a particular trait, generation time is expected to be isometrically related to other biological times such as longevity, age at first reproduction, inter-birth interval and gestation length. The generation time thus constitutes an integrative measure of the time scale at which the life cycle of a given species is completed (Gaillard et al. 2005; Staerk et al. 2019). Here, we assessed whether equids displayed longer generation times either, as a part of a generally slower pace of life compared to bovids, in which case all biological times should be isometrically associated, or whether the two groups differed in only one particular biological time such as gestation length, which would lead to longer generation times in equids than bovids. We found that all five of the biological times contributed almost equally to the bovids' pace of life, although the gestation length was slightly less tightly associated with other time-related traits (Table S9, Fig. 2A). Moreover, the generation time was equivalent to the PC1 (Fig. 2A), which means that generation time provides an overall measure of the pace of life in bovids. On the other hand, the picture was markedly different for equids. Age at first parturition, instead of generation time (Fig. 2B), was the closest to PC1 and was independent of inter-birth interval and gestation length (Table S9). Longevity was negatively associated with the overall time scale (Table S9, Fig. 2B). These findings demonstrate that, while bovids closely match the biological time syndrome hypothesis, the variation among biological times was uncoupled in equids. This suggests the existence of different selection pressures, or different constraints, on specific time-related traits between the families.

## **DISCUSSION**

229 Our findings confirm that, for a given body mass, equids live longer than bovids, whatever the  
230 metric used (maximum age at death or longevity). This difference in longevity between  
231 bovids and equids is associated with both higher survival and a delay in the onset of actuarial  
232 senescence in equids, but there is no difference in the rates of actuarial senescence. This is  
233 consistent with several recent studies highlighting that the onset of senescence has to be  
234 considered when analyzing senescence, and is more responsive than the rate of senescence  
235 (Péron et al. 2010; Hammers et al. 2013; Gamelon et al. 2014; Tidière et al. 2015), although  
236 the latter is still preferentially used in comparative analyses (e.g. Jones et al. 2008; Ricklefs  
237 2010). Moreover, the analyses of covariation among biological times in bovid and equid taxa  
238 indicate that a synchronization of all biological times evolved in bovids, whereas biological  
239 times were uncoupled in equids. This could be the result of a specific selection for longer  
240 gestation lengths in equids, a physiological constraint that prevents the evolution of shorter  
241 gestation lengths in equids, a stronger selection for a faster pace of life in bovids, or a  
242 combination of any of these factors.

243       Tooth wear is an essential process in mammalian ageing (Skogland 1988; King et al.  
244 2005), and there is evidence that tooth height is related to longevity within species (Veiberg et  
245 al. 2007). The difference in longevity we reported may be explained by a difference in a key  
246 morphological adaptation of grazers, hypsodonty. Comparison of estimates of hypsodonty  
247 index for six bovid and seven equid taxa (see Table S3) showed that equids have hypsodonty  
248 about 50% higher than bovids (difference = 2.49;  $t = 4.69$ ;  $df = 10.678$ ;  $p\text{-value} < 0.001$ , Fig.  
249 S5). Dental anatomy could, therefore, provide a mechanical explanation for the greater  
250 longevity of equids relative to similar-sized bovids, through a longer functional duration of  
251 the chewing tooth-row. It has been suggested that wear rates should be less in ruminants,  
252 because much of the chewing occurs during rumination, on material that has already been  
253 washed of grit in the forestomach (Hatt et al. 2019). However, the limited information

available has not yet demonstrated different rates of tooth wear between equids and bovids (Damuth and Janis 2014). More data like that measured in red deer (*Cervus elaphus*) by Péres-Barberia and Gordon (1998) are needed on tooth wear in free-ranging equids and grazing bovids to conclude firmly whether the greater hypsodonty in equids plays a key role in explaining their greater longevity.

The longer generation time of equids demonstrates that they have a slower pace of life than similar-sized grazing bovids. This difference of pace of life is partly due to a difference of inter-birth interval, itself caused in part by the longer gestation length of equids, and partly to their higher adult survival, which also contributes to their slow pace of life. Two different concepts exist for the occurrence of a slow pace of life. It could be the result of specific selection pressures that facilitate its evolution as a specific adaptation to resource-limited niches. Alternatively, species characterized by a slower pace of life might be displaced by species with a faster pace of life except in resource-poor niches (Vermeij 1994). There are differences in susceptibility to resource constraints between bovids and equids: the abundance of wildebeest (i.e. a grazing bovid) is much more affected by food resources than zebras (a similar-sized equid) (Grange and Duncan 2006). **Whether longer gestation periods evolved in equids from a common ancestor of the two groups, perhaps a Condylarth (Rose 1996), which had shorter gestation periods, or whether a generally slower pace of life is a characteristic of the equid lineage, cannot be determined from our study, since the common ancestor's life history is of course unknown.**

Most bovid species have an inter-birth interval of less than one year (mean of 334.00 days, 95%CI [286.54;381.46]), which allows them to produce one litter per year. On the other hand, equids display mean inter-birth intervals of about 1 year and 4 months (491.29 days, 95%CI [440.34;542.23]). The bovid life history strategy thus allows breeding seasonally to match plant phenology, which is clearly an advantage in many grassland systems. Decreasing

the gestation length may have been part of the bovid evolution towards seasonal breeding (Zerbe et al. 2012), and the shorter generation times may have allowed bovids to increase their demographic rates and abundances. This may give them an advantage in resource rich environments where predation pressure is higher than in poor environments (Melis et al. 2013). Indeed, the faster pace of life allows higher population growth rates, leading to a better demographic response to predation pressure (Grange et al. 2004). A shorter generation time allows faster evolution and this may also have facilitated their species diversity. For instance, the shorter gestation length in bovids compared to giraffids has been invoked to explain the replacement of a diverse giraffid community with a diverse bovid one over evolutionary time (Clauss and Rössner 2014).

To conclude, equids live longer than grazing bovids of similar size. This is because equids have higher survival, and their actuarial senescence begins at a later age. Equids also have greater hypsodonty, which could be a key morphological adaptation allowing greater longevity in equids, though more data are needed on wear rates in the wild to reach a firm conclusion. Grazing bovids have a faster pace of life, with shorter gestation periods. The shorter gestation periods of bovids may be associated with accelerated rates of intrauterine growth (Baur 1977), although the morphological and physiological mechanisms involved remain to be discovered. This scenario considers equids to be constrained by slower intrauterine growth and a slower pace of life, which makes them mainly competitive in environments with limited resources. Alternatively, a longer gestation length for equids may be a specifically evolved adaptation to increased survival in these environments. The fast pace of life in bovids may be a key to the rapid evolution of the bovids since the Miocene; today they dominate communities of grazing animals, in species diversity and in abundance.

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454 **Table 1.** Parameter estimates from the linear models of the relationship between survival (i.e.  
455 maximum age at death, longevity, and adult survival rate) or actuarial senescence (i.e. onset  
456 and rate of senescence) metrics and the mean female adult body mass among 23 taxa of large  
457 herbivores belonging to two orders of mammals.

		$\beta$	95% CI	t value	Adjusted-R <sup>2</sup>
<b>Maximum age at death</b> N= 23 taxa	Intercept	2.496	2.033; 2.960	10.56	0.61
	Order ( <i>Equidae</i> )	0.225	0.133; 0.318	4.79	
	Adult body mass	0.142	0.059; 0.225	3.34	
<b>Longevity</b> N= 23 taxa	Intercept	1.787	1.234; 2.341	6.33	0.63
	Order ( <i>Equidae</i> )	0.225	0.115; 0.335	4.01	
	Adult body mass	0.228	0.129; 0.328	4.50	
<b>Adult survival rate</b> N= 19 taxa	Intercept	1.050	-0.224; 2.324	1.62	0.47
	Order ( <i>Equidae</i> )	0.385	0.153; 0.617	3.25	
	Adult body mass	0.321	0.097; 0.544	2.81	
<b>Onset of senescence</b> N= 19 taxa	Intercept	2.056	1.845; 2.267	19.08	0.34
	Order ( <i>Equidae</i> )	0.498	0.191; 0.804	3.18	
<b>Rate of senescence</b> N= 19 taxa	Intercept	-0.926	-2.123; 0.271	-1.52	0.31
	Onset	0.791	0.276; 1.305	3.01	

458

459 **Table 2.** Parameter estimates from the linear models of the relationship between biological  
460 times and the mean female adult body mass among 23 taxa of large herbivores belonging to  
461 two orders of mammals.

		$\beta$	95% CI	t value	Adjusted-R <sup>2</sup>
<b>Generation time</b> N= 12 taxa	Intercept	0.107	-0.668; 0.881	0.27	0.78
	Order ( <i>Equidae</i> )	0.179	0.002; 0.356	1.98	
	Adult body mass	0.310	0.156; 0.464	3.95	
<b>Gestation length</b> N= 15 taxa	Intercept	4.844	4.542; 5.146	31.42	0.89
	Order ( <i>Equidae</i> )	0.243	0.179; 0.307	7.44	
	Adult body mass	0.143	0.087; 0.200	4.99	
<b>Inter-birth interval</b> N= 12 taxa	Intercept	5.050	4.260; 5.840	12.53	0.72
	Order ( <i>Equidae</i> )	0.295	0.115; 0.476	3.21	
	Adult body mass	0.150	-0.006; 0.307	1.88	
<b>Age at first parturition</b> N= 14 taxa	Intercept	5.582	4.670; 6.494	12.00	0.39
	Adult body mass	0.260	0.094; 0.426	3.07	

462

463 **Figure legends**

464 **Figure 1.** Relationship between maximum age at death (A), longevity (B), or adult survival  
465 (C) and taxon-specific body mass of adult females for 13 bovids (open dots) and 10 equids  
466 (full dots). For a similar body mass, equids live longer and have a higher adult survival than  
467 bovids.

468 **Figure 2.** Normed Principal Component Analyses performed on 5 biological times for 5 bovid  
469 and 7 equid taxa separately. All biological times are positively correlated among bovids,  
470 whereas for equids there is an uncoupling of biological times.